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BOTANICAL GAZETTE

FEBRUARY, 1904

ON A SELF-RECORDING METHOD APPLIED TO THE MOVEMENTS OF STOMATA.

FRANCIS DARWIN.

(WITH FIFTEEN FIGURES)

IN my paper on stomata¹ it was incidentally shown that the temperature of a leaf varies, other things being equal, with the condition of the stomata. Thus if there are two leaves, in one of which (O) the stomata are open, while in the other (C) they are closed, it is found that O is cooler than C. It is evident that this must be so because the evaporation from O is greater than that from C; in fact, one corresponds to the wet bulb, and the other to the dry bulb of a psychrometer. In the experiments above referred to the leaves employed were those of *Tropaeolum*, C being a leaf in which the stomata were closed by separating it from the plant, and thus allowing it to wither; while O was a leaf still attached to the plant, with normally open stomata. As the stomata of O closed in the evening, its temperature approached more and more to that of C, and to that of the dry bulb thermometer, while the temperature of an aquatic leaf (of a species in which the stomata are open at night) remained cooler than the dry bulb thermometer.

These experiments suggested that the changes in the temperature of a leaf might be used, with certain precautions, as an index of the condition of the stomata. It was hoped that by the use of this method it would be possible to check and control

¹ DARWIN, FRANCIS, Observations on stomata. Phil. Trans. Roy. Soc. London B. 190: 582. 1898.

observations made by the horn hygroscope, as given in the above-quoted paper.

METHOD.

The apparatus employed was one of Callendar's recorders, a platinum thermometer,² or resistance thermometer, in which the difference between the temperatures of two fine platinum wires is recorded on a revolving drum.³ In the experiments illustrated by *figs. 1, 2, 3, 5, 6, 12, 13, 14, 15*, the resistances were so arranged that a vertical fall of 24^{mm} in the tracing made represents a difference of 1° C. But as some of the figures have been reduced in scale it is simpler to state that the distance between the horizontal lines represents one-sixth of a degree C. In *figs. 4, 7, 8, 9, 10, 11*, the value of 1° C. is uncertain, owing to an omission in my notes. In these figures the distance between the horizontals represents either 0.1° or 0.2° C.

The fine platinum wires, the difference of whose temperature is recorded, are disposed in fine zigzags on plates of talc 10×3^{mm}, which will be referred to as "bulbs." The leaf is inverted, so that its stomatal surface is free, and its astomatal surface is in contact with the wire. It is generally necessary to hold the petiole in a clamp, and to press the leaf against the bulb by a pair of springs, or by a thread having weights at each end. An unavoidable drawback of the apparatus is that, owing to the current run-

² The instrument was made by the Scientific Instrument Company at Cambridge. I am much indebted to my brother, Horace Darwin, for help in management of the apparatus.

³ A resistance thermometer, or, as it is often called, a platinum thermometer, consists of a fine platinum wire, which is exposed to the temperature it is desired to measure. As its temperature alters, its electric resistance also alters, and by measuring this resistance the temperature is found. These thermometers are usually made of platinum, but this is not necessarily the case; a fine wire of copper or of other metal can be used in many cases with equally good results. The resistance is usually measured by a Wheatstone bridge; the Callendar recorder is an automatic Wheatstone bridge, which is continually measuring the resistance, and at the same time moves a pen so that its distance from a fixed point is proportional to the temperature. This pen marks a line on a drum driven by clock-work, and thus a curve is drawn giving a continuous record of the temperature of the thermometer. By the use of two resistance thermometers a curve can be made representing the difference of their temperatures, and this is the arrangement which I have employed. See Callendar *Electric Recorders*, a pamphlet published (1901) by the Cambridge University Press.

ning through the wires, the bulbs are warmer, by roughly 2° , than the surrounding air. Thus the leaf under experiment is not in strictly natural conditions, being constantly warmed; in spite of the artificially increased transpiration⁴ due to this condition,

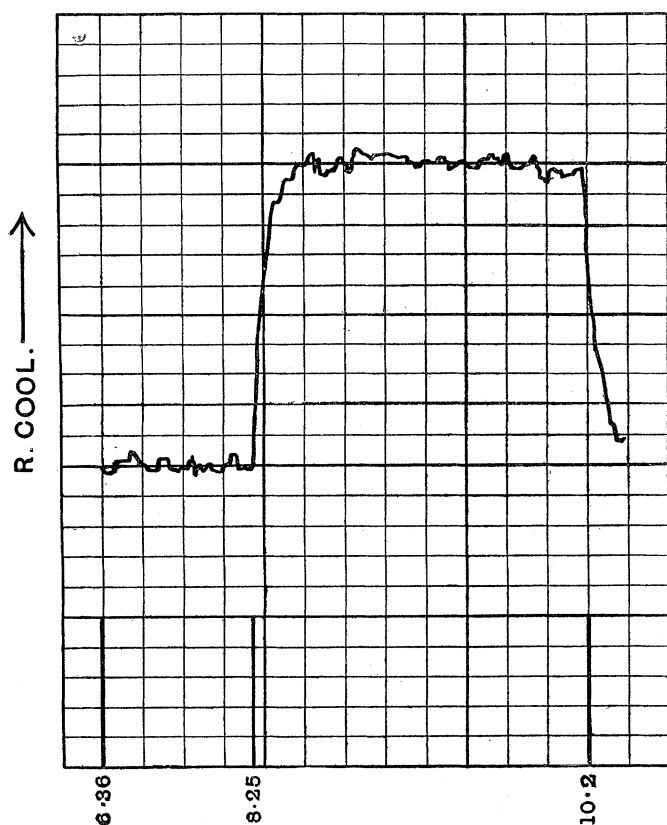


FIG. 1.—See Experiment 83 B, p. 84.

the leaf behaves normally in showing a marked rise in temperature as the stomata shut. Nor does the warming of the leaf,

⁴ By the use of the horn hygroscope it is possible to show that the part of a leaf in contact with the recorder bulbs transpires more than the unheated parts of the same leaf. The following are readings taken on a tulip leaf, February 22, 1901, B being the transpiration of the part of the leaf in contact with the bulbs, N of the normal parts of the leaf.

P. M.		N	B
4:53	- - - - -	30	40
10:43	- - - - -	23	30

generally speaking, prevent the stomata showing normal behavior, *e. g.*, in closing at night, or by artificial darkness during the day, or again when the petiole is divided and the leaf begins to wither.

The purely physical results of the warmth of the bulbs have also to be considered. Supposing the apparatus is in equilibrium, and the pen therefore is running along the zero line, indicating equality of temperature in the bulbs; if a bad conductor, such as a flock of cotton wool be placed on one bulb, the pen will instantly be deflected, as shown at 8:25 P. M., *fig. 1*.

EXPERIMENT 83 B, *fig. 1. July 2, 1900. COTTON WOOL.*

P. M.

6:36-8:20 Nothing on either bulb.

The battery turned off, and a thick pad of cotton wool placed on bulb B; this prevents loss of heat from B, and therefore gives an R-cool⁵ movement when the battery was turned on.

8:25 Battery on: result, an R-cool rise of about 1.7° C.

10:2 Wool removed: result, an R-warm fall.

In the same way, if a good conductor, *e. g.*, a thin metal plate or a withered leaf, is placed on bulb R, the result shown at 5:56 in *fig. 2* will be seen; the effect of its removal is seen at 8:28.

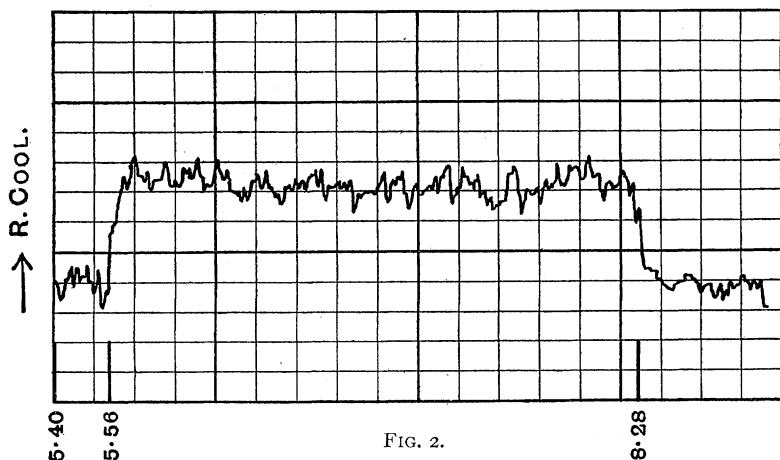


FIG. 2.

It is clear that these facts must be taken into account in experiments on leaves. This difference in temperature would not in

⁵The two bulbs of the thermometer are distinguished as bulb B and bulb R. When the pen is deflected from the zero line it indicates a difference of temperature between B and R which may be called a "B-warm" or "R-cool" effect; while a contrary effect would be described as either "B-cool" or the equivalent "R-warm."

any way indicate the cooling effect of transpiration, because the leaf used is one cut from the parent plant, in which the stomata had closed; the leaf simply acts as a good conductor.

In most experiments a leaf with stomata shut was placed on the control bulb, the experimental leaf being on the other. This has not merely the advantages pointed out, but it has the more important effect of protecting the control bulb from draughts of air, and therefore from changes in temperature. The effect is evident when both bulbs are covered with cotton wool. The line drawn is then quite free from the zigzags so evident in the figures published. The following experiment shows that it is important to choose carefully the body placed on the control bulb.

EXPERIMENT 46, *fig. 3, Dec. 18, 1899.* DRY AND WET GYPSUM.

A small block of dry gypsum wrapped in tin-foil on bulb R; a similar block soaked in water on bulb B; the tin-foil was pierced with pin holes so as to allow only a moderate degree of evaporation.

A. M.

11:7 Battery on to balance, and then turned off so that the blocks of gypsum might be placed on the bulbs.

11:25 Battery on: the B-cool fall is owing to the evaporation and conducting power of the damp gypsum (B).

P. M.

12:14 Doors and windows of the greenhouse opened, producing the following changes:

			Dry bulb, °C.	Wet bulb, °C.	Humidity of air, per cent.
12:13	-	-	15.0	12.2	70
12:18	-	-	11.3	7.8	58
12:27	-	-	8.5	6.0	66
12:43	-	-	7.8	6.0	75

The air was thus cooled, and was at first rendered drier; the increased evaporation should therefore have cooled B still more, but the curve shows that it became relatively warmer; this must be due to the fact that the block of damp plaster (B) took longer to cool. It was clearly a temporary effect, since at 12:43 the curve returned to nearly the position occupied before the temperature was lowered.

At 12:43 (about) the windows and doors were shut, and a reverse movement of the same temporary character followed.

The experiment was repeated with an *Alisma* leaf on bulb B and the damp block of plaster on R. When the temperature fell, the leaf, in spite of its smaller volume, cooled more slowly than the plaster; there was therefore a relative warming of the leaf lasting about 15 minutes, and the reverse effect occurred as

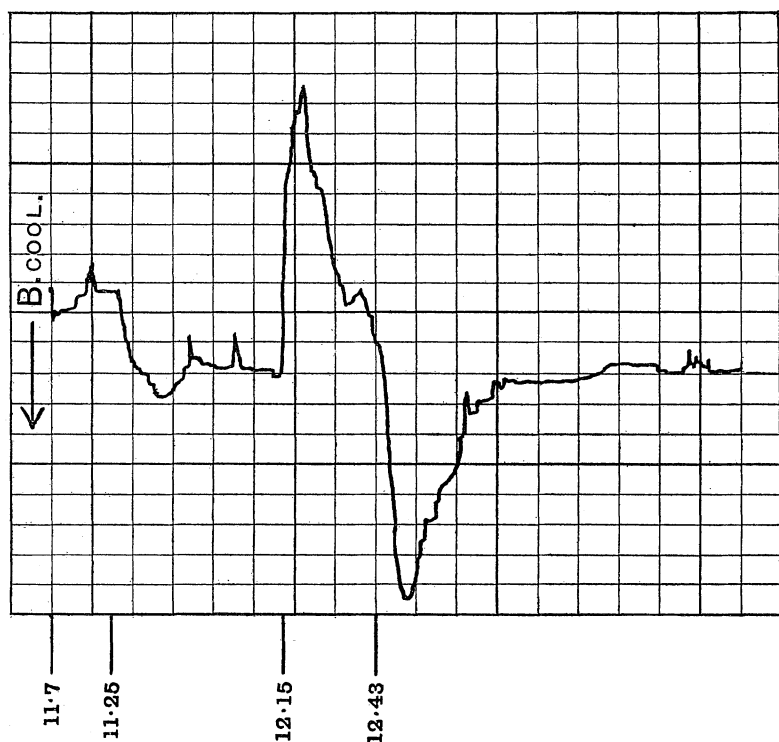


FIG. 3.—See Experiment 46, p. 85.

the air became warmer again on the door and windows being closed.

These experiments show clearly the necessity of using for the control bulb a body equaling in volume and conductivity that on the experimental bulb. A cut leaf with closed stomata answers this purpose well enough.

Another element of some importance is the condition of the air. It is obvious that, if the air becomes drier, the evaporation from the experimental leaf will increase, and the curve might be

interpreted to mean that the stomata had opened more widely. This is not of great practical importance, since the method is used chiefly to demonstrate sudden changes in the condition of the stomata. But in taking readings of the closure of the stomata occurring naturally at night, it would be necessary to take account of the effect of the dampness of the night air. One way of counteracting the error is to place on the control bulb a leaf of a species whose stomata do not close at night. Another method, which is more easily managed, is to use for a control a wet strip of linen.⁶ Any change in the moisture of the air will affect both leaf and linen in roughly the same way, and thus an increase in the leaf temperature may be put down as practically all due to closure of the stomata. It should be noted that the effect of moist air is not nearly so great in a resistance thermometer as in an ordinary wet and dry bulb thermometer, no doubt because the temperature of the bulbs is maintained above that of the air. It follows that the error against which the use of a wet bulb is meant to guard is not nearly so great as might be expected.

EXPERIMENT 106. *March 14, 1901.*

Bulb B was covered with a strip of wet linen, while bulb R was exposed to the air. By watering the floor and the hot pipes, the air was made damp, as shown by the following readings:

P. M.			°C.	°C.	Per cent.
4:0	-	-	15.7°	12.7°	68
Watered floor					
4:5	-	-	15.8	13.2	
4:7½	-	-	15.8	14.0	83
4:12	-	-	16.0	15.0	89
4:19½	-	-	16.0	15.2	91
5:11	-	-	14.9	12.8	77

Between 4:0 P. M. and 4:19½ P. M. the difference between the wet and dry bulb mercury thermometers decreased from 3.0° C. to 0.8°, *i. e.*, by 2.2°. If the resistance thermometers behaved like an ordinary wet and dry bulb psychrometer, the difference

⁶It must be separated by a layer of oil-silk from the surface of the bulb, lest the thermometer wire should be wetted through a crack in the varnish by which it is covered.

between their temperatures, as seen on the curve, should have diminished by 53^{mm}. As a fact it only diminished by 14^{mm}, *i. e.*, the effect as measured by the Callendar recorder is only 26.4 per cent. of the actual change. Between 4:19½ and 5:11 the difference between wet and dry bulbs increased (as the air grew drier again) from 0.8° to 2.1°, *i. e.*, by 1.3° C. This should have given a change on the recorder-curve of 31^{mm}. The recorded change was not at any rate more than 8^{mm}, *i. e.*, 25.8 per cent. of the actual psychrometer effect.

EXPERIMENT 108. *March 16, 1901.* NARCISSUS.

In this experiment the effect of damp air is shown with a Narcissus leaf on bulb R and with nothing on bulb B. The floor and hot pipes were watered, with the following result:

P. M.		Dry, °C.	Wet, °C.	Per cent.
2:11	- -	17.9	12.7	52
		Watered floor and pipes.		
2:22	- -	18.3	16.8	85
2:27	- -	18.2	17.2	90
2:56	- -	Opened door.		
3:1	- -	16.8	13.5	67

Thus, between 2:11 and 2:27, the difference between the wet and dry bulb mercury thermometers decreased from 5.2° to 1.0°, *i. e.*, by 4.2°. This would mean a fall in the curve of 100.8^{mm}. The actual change in the curve was a drop of 22^{mm}, or in round numbers 22 per cent. of the psychrometer difference. The stomata were wide open throughout the experiment. Between 2:27 and 3:2 the difference between wet and dry mercury thermometers increased by 1.7°, which would equal 41^{mm}; the change in the curve was 12^{mm}, or 29 per cent. of 41^{mm}.

It should be added when an ordinary thermometer is converted into a wet bulb by wrapping it in a leaf, the difference between it and a dry bulb is considerably less than that between the wet and dry bulbs of a psychrometer.⁷

It is not obvious why the leaf when wrapped around the bulb of a thermometer behaves so differently from the wet gauze with which the psychrometer is covered. But the cause, whatever it

⁷ DARWIN, FRANCIS, Observations on stomata. Phil. Trans. Roy. Soc. London. B. 190: 583. 1898.

is, should affect the recorder bulbs in the same way. On the whole, we may conclude that the effect of variations in the humidity of the air on the temperature of a leaf fitted to the recorder is comparatively small, especially when counteracted by the use of a layer of damp linen on the control bulb of the instrument. And this must be some advantage in experiments like the present, in which it is sought to estimate the opening and shutting of the stomata by temperature changes.

A possible source of error, in long-continued experiments, is that a leaf will transpire less in darkness than in light, quite apart from the closure of the stomata. This is believed to be due to the fact that the radiant energy absorbed by the chloroplasts is in part made evident as heat. It follows that a relative rise of temperature occurring at night might be put down to closure of the stomata, when it might in reality be due to the checking of "chloro-vaporization" by darkness. The following experiment, however, shows that this is not a serious source of error.

EXPERIMENT 102. *February 22, 1901.*

A tulip leaf (attached to the plant) was placed on bulb R, an "artificial leaf" made of wet linen on bulb B. Readings with the horn hygroscope showed that the stomata were open from 4 P. M., when the experiment began, until 10:32 P. M.; a slight closure had occurred, but the nocturnal reading corresponds to a fair amount of transpiration. The temperature of the air fell during the same period from 18.2° to 16.6°, but the relative moisture of the air remained the same, *i. e.*, 60 per cent. The reading of the resistance thermometer remained almost constant.

As far as one experiment may be trusted, it would seem therefore that darkness, apart from its effect on the stomata, need not produce any serious check to transpiration.

THE EFFECT OF WITHERING.

One of the points investigated in my work on stomata (*loc. cit.*, p. 548) was the phenomena which occur when certain leaves are severed from the plant. The first effect is that the stomata open more widely, and this "preliminary opening" is followed by a gradual closure of the stomata. This seemed a good subject for the recording method, since the effects occur rapidly,

and errors from changes in external circumstances are not likely to obscure the result.

The following diagrams give some of the results obtained. It will be seen that the effect of cutting the leaf stalk is a practically instantaneous fall of temperature, corresponding to the preliminary opening of the stomata, followed by a gradual rise toward the zero line. The results, in fact, absolutely confirm the observations made with the horn hygroscope.

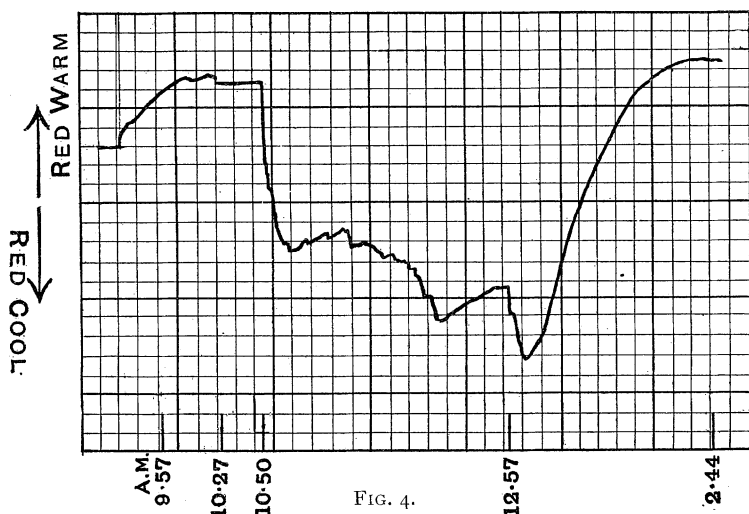


FIG. 4.

EXPERIMENT 27, *fig. 4.* April 24, 1899. *CAMPANULA PYRAMIDALIS.*

A. M.

9:57-10:27 Zero-line drawn, *i. e.* nothing on either bulb. Battery turned off and an attached leaf placed on the bulb R, a withered leaf being placed on the bulb B.

10:50 Battery turned on; the R-cool fall in the curve indicating the difference between the transpiring and withered leaf.

10:50-12:57 An irregular R-cool fall due to the stomata on the attached leaf (R) opening, as indicated by the horn hygroscope. Between 10:48 and 12:54 the moisture of the air decreased from 70 per cent. to 61 per cent., so that the whole of fall in the curve was not due to the opening of the stomata.

P. M.

12:57 Leaf on bulb R severed: a sudden R-cool fall lasting for about 10 minutes, followed by R-warm rise lasting for $1\frac{1}{2}$ hours. It will be noticed that the preliminary opening of the stomata (12:57) takes place during a slight rise in the curve (R-warm) and is thus rendered distinct.

EXPERIMENT 51, *fig. 5. December 25, 1899. EUPATORIUM WEINMANNIANUM.*

An attached Eupatorium leaf on the bulb R; an attached Alisma leaf on the bulb B.

12:21 Eupatorium severed; rapid R-cool rise lasting 6 or 7 minutes, followed by an R-warm fall, lasting 24 minutes.

The following experiment shows the same result occurring slowly in an aquatic plant, in which class the stomata, as is well known, close much less effectively or in some species not at all, as the leaves wither.

EXPERIMENT 52, *fig. 6. January 16, 1900. ALISMA.*

Attached Alisma on bulb B; withered Eupatorium on R.

A. M.

10:28 B-cool fall showing difference between the transpiring Alisma and the partially withered Eupatorium leaf.

11:54 Alisma cut: an immediate B-cool fall showing opening of stomata, lasting for about half an hour, followed by gradual closure (B-warm) lasting more than $3\frac{1}{2}$ hours.

The following readings of the horn hygroscope show that the Alisma stomata were not fully shut even towards the end of the period of closure. In this experiment the stomata of the Eupatorium leaf were not quite shut at the beginning of the experiment, though the low reading (10) of the horn hygroscope shows that they were nearly shut, nor were they quite shut even at 3 P. M. The withering of the leaves of this species is, I think, somewhat capricious.

READINGS WITH THE HORN HYGROSCOPE.

A. M.	*	Alisma	Eupatorium	Difference
11:53	- - -	32	10	22
11:54	- - - -	Cut Alisma.		
11:56	- - -	40	11	29
12:23	- - - -	40	9	31
12:42	- - -	35	9	26
P. M.				
2:11	- - - -	25	8	17
2:57	}	22	7 (avg. of 2)	15
3:00				

The difference between the horn hygroscope readings of the two leaves is given in the dotted line (*fig. 6*) and agrees fairly with the temperature curve.

It should be noted that the closure of the Eupatorium stomata would not increase but slightly diminish the long B-warm rise; on the other hand the fall of the curve from 11:54 to 12:24 is to a very slight degree increased by the change in the Eupatorium leaf during that period.

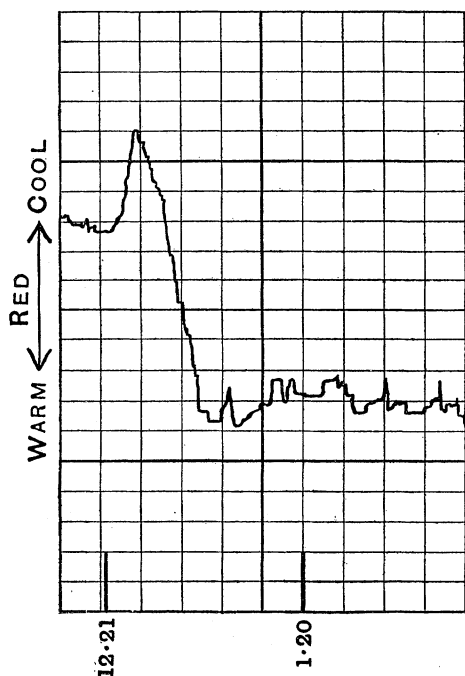


FIG. 5.—See Experiment 51, p. 91.

THE EFFECT OF DRY AIR.

Stahl⁸ has published experiments from which he draws the conclusion that the closure of the stomata in dry air does not depend on the general diminution of the store of water in the leaf, but rather on the loss of water by the guard cells, which may, in his opinion, be independent of the general withering of the leaf. I have discussed this difficult question in my *Observations*,⁹ where I have tentatively given the theory that the guard cells lose turgor “spontaneously,” *i. e.*, “not by simple evaporation, but in response to a stimulus. And this stimulus may be the slight flaccidity of

the rest of the leaf.” This point of view, though it does not harmonize with Stahl’s facts, has nevertheless some probability. According to my view, there must be, whenever the stomata close, a slight, though it may be an imperceptible, general deturgescence of the leaf. The repetition of certain experiments with the horn hygroscope confirms me in my belief that the first stage in the closure of the stomata is a slight general withering,

⁸STAHL, Bot. Zeitung, Einige Versuche über Transpiration und Assimilation. Bot. Zeit. 52^r: 121. 1894.

⁹DARWIN, FRANCIS, Observations on stomata. Phil. Trans. Roy. Soc. London B. 190: 617. 1898.

and not a direct specialized reaction of the stomata to dryness of the air. I undertook these experiments in consequence of reading Aloi's papers,¹⁰ with which I was unacquainted when I wrote my *Observations on stomata*. The point of Aloi's work is his proof that leaves exposed to a very dry atmosphere may have widely opened stomata, if the plants are well watered.

My experiments were carried out as follows: A plant is placed under a water-sealed bell jar, *i. e.*, in a very moist atmosphere.

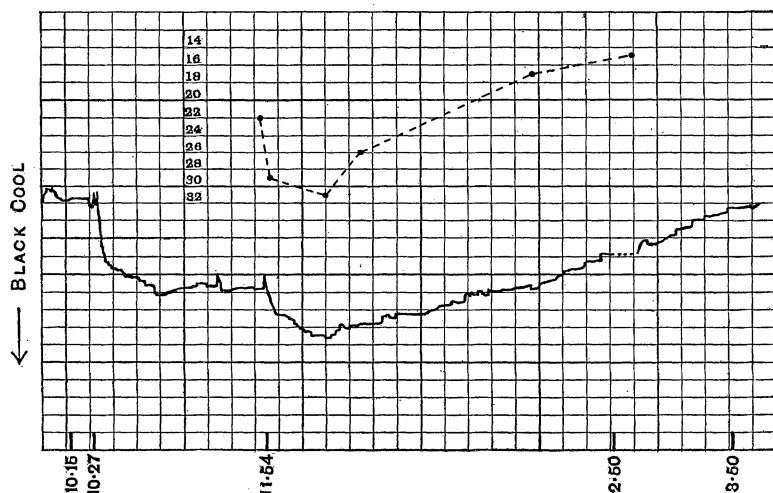


FIG. 6.—See Experiment 52, p. 91.

The bell is removed, and a reading with the horn hygroscope taken at once; the plant is then left in the dry air of a room, and it is found that the stomata gradually close, in spite of the illumination remaining practically unchanged. This is the class of experiment recorded in *Observations on stomata*. The new fact brought to my notice is that the result often fails with plants growing in well-watered soil, while it succeeds more uniformly with plants in which the soil is dry. This points to the conclusion that the closure of the stomata depends on the loss of water in the plant as a whole being greater than the intake. Analogous

¹⁰ ALOI, La traspirazione delle piante terrestri, etc. Catania, 1891. ALOI, Influenza dell' umidità del suolo sulla traspirazione, etc. Naturalista Siciliano 13: —, (Ni. 4-9.)

results were also obtained with the recorder (see *fig. 12*), but it will be convenient to preface them by the simpler experiments in which the condition of the soil is not taken into account.

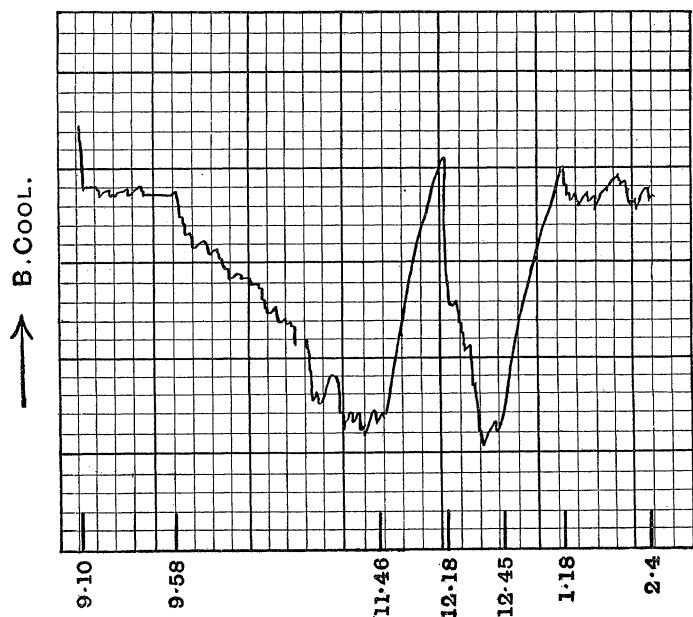


FIG. 7.

EXPERIMENT 23, *fig. 7.* March 10, 1899. CAMPANULA.

- | | |
|-------------|--|
| A. M. | |
| 9:10 | Zero line drawn. |
| 9:58 | Attached leaf on bulb R. Cut leaf (stomata shut) on bulb B. |
| 9:58-11:46 | Temperature of attached leaf on R sinks as stomata open more widely. |
| 11:47 | Plant moved from damp greenhouse (T. 19°, Psy. 78%) to dry greenhouse (T. 21.2°, Psy. 52.8%). |
| P. M. | |
| 11:47-12:18 | Temperature of R rises (closure of stomata). |
| 12:18 | Plant moved to damp house (T. 19.6°, Psy. 81%). |
| 12:18-12:38 | Temperature of R sinks as stomata open. |
| 12:45 | Plant moved to dry house (T. 22.9°, Psy. 51.5%). |
| 1:18 | The temperature reading practically the same as the zero line at 9:58 (<i>i.e.</i> , before the leaves were placed on the bulbs). This is also true at 12:18; the inference being that in the dry air the stomata closed so completely that the temperature of the attached leaf (R) was the same as that of the cut and withered leaf (B). |

The temperature difference recorded is about 36^{mm} or 1.5°C . It must be noted that at 11:46 A. M. or 12:38 P. M. when the plant was placed in dry air the effect of such change, if the stomata were immovable openings, would be to cool the attached

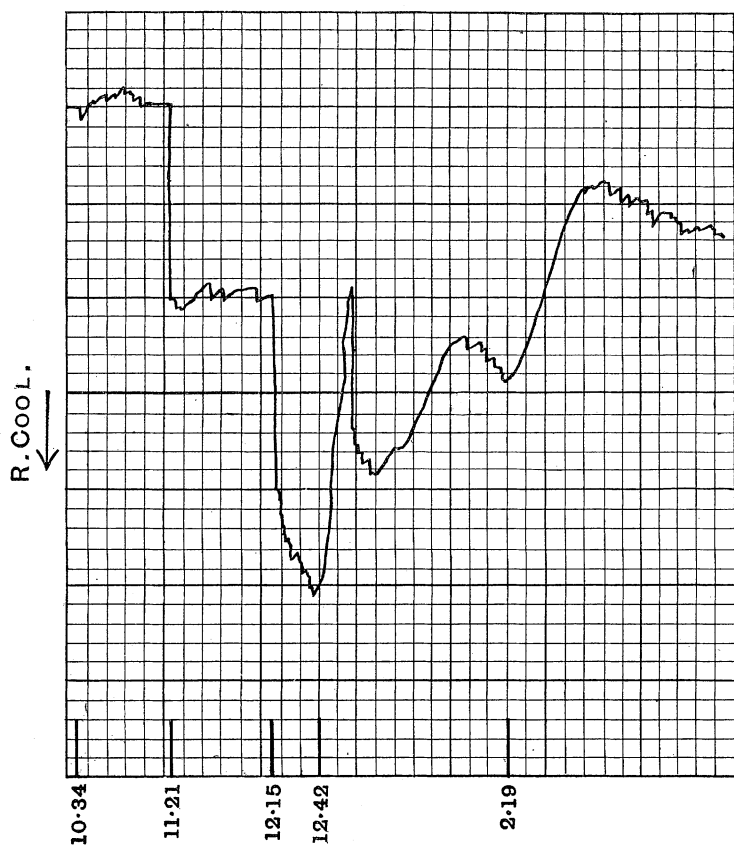


FIG. 8.—See Experiment 26, p. 96.

leaf R still more. The stomata, therefore, must have closed at once.

It may be suspected that, the damp house being some 3° cooler than the dry one, the rises of temperature at 12:18 and 12:38 were due to leaf R assuming the temperature of the air in the dry house more quickly than B. But if this were the case, the temperature curve between 1:18 P. M. and 2:4 P. M. when both

leaves were left on the recorder bulbs would have fallen to what it was at 12:38, as the leaves became equal in temperature. Inequality in assuming a given temperature is a genuine source of error, as appears at p. 85, but in the present case it cannot be admitted.

EXPERIMENT 26, *fig. 8.* March 21, 1899. CAMPANULA.

A. M.

10:34-11:21 T. at 10:34 13.7°, Psy. 88%. Zero line drawn; nothing on either bulb.

11:21 T. 15.0°, Psy. 75%. Attached leaf on bulb R. Withered leaf on bulb B.

P. M.

12:16 T. 21.2°, Psy. 47%. Plant removed to dry greenhouse. The first effect of the dry air is a considerable fall in temperature (R-cool).

12:42-2:25 T. 24.5-21°, Psy. 43-48%. An irregular rise indicating a partial closure of stomata.

2:19 (T. at 2.40 21°, Psy. at 2.40 58%) A further closure of stomata, owing probably to the darkening effect of a snow-storm.

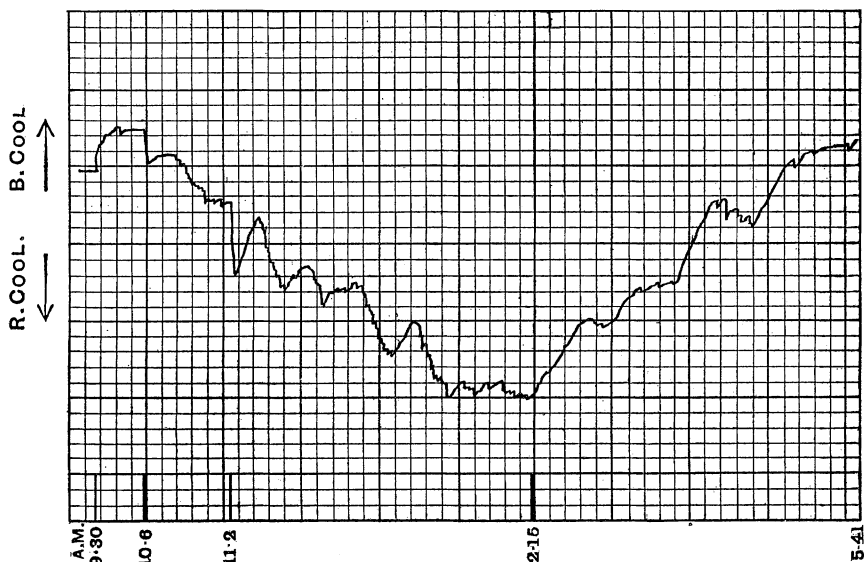


FIG. 9.— See Experiment 15, p. 97.

EXPERIMENT 15, *fig. 9.* February 21, 1899. TROPAEOLUM.

- A. M.
 9:30-10:6 Zero line drawn, nothing on either bulb.
 10:6 Attached leaf on bulb R, withered leaf on B.
 10:6 T. 12-13°, Psy. 77-78%. A gradual opening of stomata till 11:2.
 11:2 Plant moved to dry greenhouse (T. at noon 25°, Psy. 40%). A sudden R-cool move, owing to increased evaporation but there was no sign of a permanent R-warm move (which would have indicated a closure of the stomata) until 2:15, although the air remained very dry, *e. g.*, at 3 P. M. Psy. 35%, T. 24.1°, and at 5:2 P. M. the psychrometer still gave 40% and the temperature was 23.5°. The rise of the curve (R-warm move) was probably due to a genuine withering of the attached leaf, though the horn hygroscope did not indicate any closure even at 3 P. M.; at 5:40 the temperature curve shows complete closure, and this is confirmed by a horn reading at 5:50.

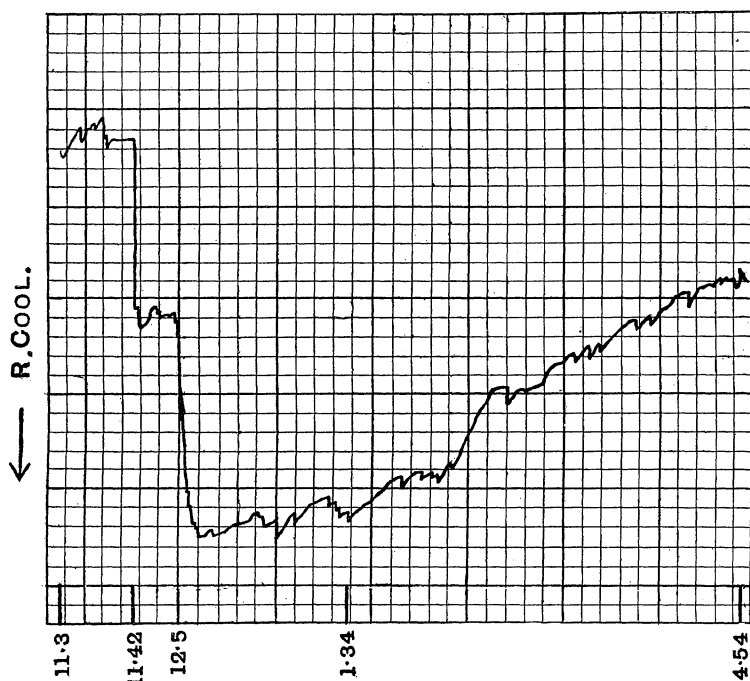


FIG. 10.—See Experiment 17 B, p. 98.

EXPERIMENT 17 B, *fig. 10. February 23, 1899. NICOTIANA AFFINIS.*

A. M.

- 11:3-11:42 Zero line (nothing on either bulb). T. at 11:8 19°, Psy. 74%
 11:42 Attached leaf on bulb R, withered on B.

P. M.

- 12:5 Plant placed in dry greenhouse. T. 27°, Psy. 41%. Rapid R-cool move owing to the physical effect of the dryness of the air.
 1:34-4:54 Gradual R-warm move, indicating gradual closure of stomata. The occurrence of closure was confirmed by horn hygroscope readings.
 4:49 T. 23.6°, Psy. 37%.

EXPERIMENT 16, *fig. 11. February 24, 1899. EUPATORIUM WEINMANIANUM.*

No zero line drawn, but the beginning of the curve is roughly zero.

A. M.

- 11:39 Attached leaf on bulb R; withered leaf on bulb B. T. at 11:35 20.6°, Psy. 71%.

P. M.

- 12:40 Moved plant to dry greenhouse. T. 30.8°, Psy. 40%. A rapid R-cool move, owing to physical effect of the dry air.
 1:2 A rapid R-warm move, indicating partial closure of the stomata.
 2:52 T. 33°, Psy. 42%. A young leaf on the plant showed signs of being withered, but the experimental leaf not visibly flagging; nevertheless it must have been suffering from want of water, as it showed no sign of opening its stomata on being placed in damp air.

Here follow two experiments on the different behavior of dry air on plants well and badly supplied with water in the soil.

EXPERIMENT 87, *fig. 12. July 25, 1900. TROPAEOLUM MAJUS.*

Two pots of *Tropaeolum*, viz., R and B; of these, plant R had been kept well watered; B had been kept without water, but was not so dry as to produce closure of the stomata.

A. M.

- 9:39 An attached leaf of plant R placed on bulb R. An attached leaf of plant B placed on bulb B.
 10:28 The horizontal line ending here shows that the well-watered leaf R was considerably the cooler. The leaves were now removed from the recorder, and plant B placed in damp air under a bell-jar.
 11:18 Plant B removed from damp air, and again placed on bulb B; leaf B, badly watered, is now cooler than it was; this can only be due to the stomata being more open; the difference cannot be due to the physical effect of the bell-jar, where, owing to the check to transpiration, it would have been warmer than leaf R, still exposed to the air of the greenhouse. T. 23-28°, Psy. 67-58%.

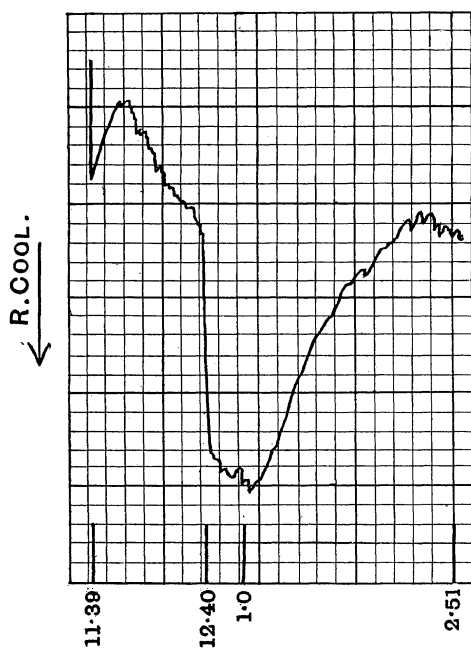


FIG. 11.—See Experiment 16, p. 98.

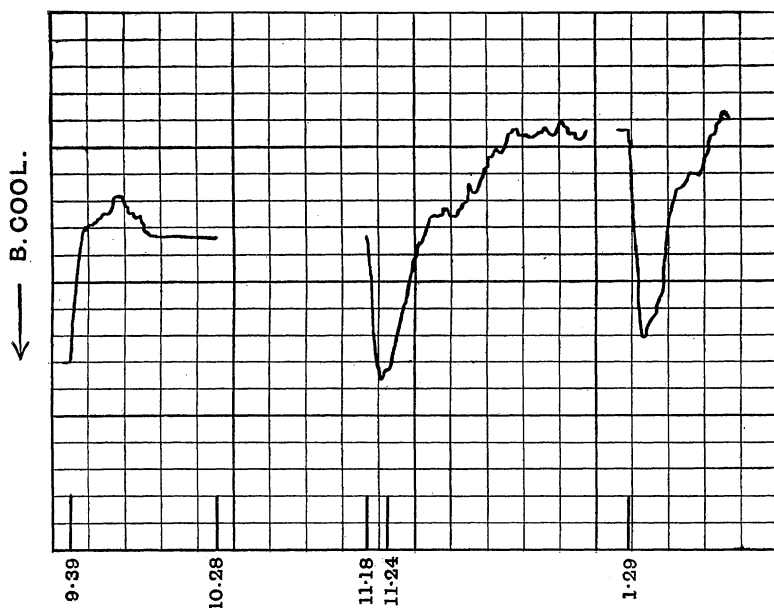


FIG. 12.—See Experiment 87, p. 98.

- 11:24 Sudden change, indicating a rise of temperature in B or fall in R, and as there is no reason to suppose that any change in R had taken place, the rise in the curve must be due to the closure of the B stomata in the drier air of the greenhouse.
- P. M.
12:31 Plant B again placed in damp air.
- 1:29 Leaf B again placed on pyrometer B. Again the curve indicates that the stomata were more open and rapidly close in dry air. The opening of the stomata in the damp, and the closure in the dry air, was observed in this experiment by means of the horn hygroscope, and these approximately follow the temperature curve.

The above results were confirmed by two more observations on the same *Tropaeolum* plants. In both cases the stomata of a leaf on the unwatered pot B were opened by damp air. Judging by the temperature curve only, in one case the dry air produced rapid and striking closure, in the other, slow and less obvious closure.

These experiments are not thoroughly satisfactory, since both the well watered and unwatered plants should have been exposed to alternations of dry and damp air; but they show at any rate a degree of sensitiveness to such changes in the unwatered plant which I have not observed in normal plants.

COMPRESSION OF THE STEM.

It is known¹¹ that compressing the stem in a vise checks the transpiration current. And I have shown¹² that the checked water supply produces closure of the stomata, which apparently reopen when the vise is unscrewed. The following is a temperature record of the same experiment:

EXPERIMENT 97, *fig. 13*. August 23, 1900. CLEMATIS MONTANA.
A branch placed with the cut end in water.

- A. M.
10:23 A leaf on bulb B, an artificial leaf on R.
10:49 Vise screwed tightly to branch below the leaf.
The first effect is a B-cool move, indicating the preliminary opening observed (*loc. cit.*) with the horn hygroscope; followed by a closure of the stomata (B-warm).

¹¹ DARWIN, FRANCIS, and PHILLIPS. Proc. Cambridge Phil. Soc. 5:364. 1886.

¹² DARWIN, FRANCIS, Observations on Stomata. Phil. Trans. Roy. Soc. London B 190:555. 1898.

11:55 Vise unscrewed.

The final result is B-cool, *i. e.*, opening of the stomata; the preliminary increased closure, lasting about five minutes; I have not observed elsewhere, and is no doubt the expression of the fact that release from compression does not at once take effect.

P.M.

1:22 Vise again applied.

Preliminary opening followed by closure.

2:19 Vise removed. No effect. This no doubt is due to the vessels being so much crushed that their lumens remain closed even when relieved from compression. In a second experiment on Aug. 24, 1900 with another branch of *Clematis montana* the preliminary opening, 12 minutes, and closure, 24 minutes, were clear, but the effect of removing the vise was very slight. When, however, the branch was cut under water between the vise and the leaf, an immediate cool-move occurred.

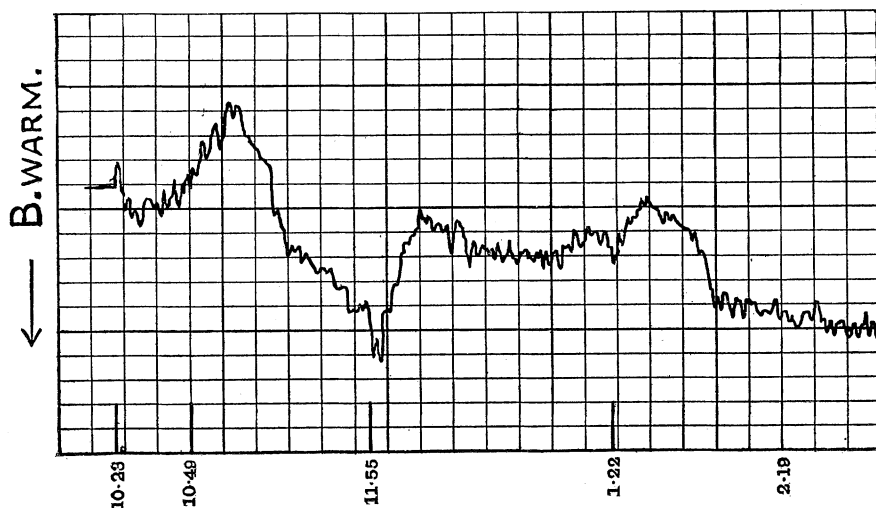


FIG. 13.—See Experiment 97, p. 100.

I have discussed (*loc. cit.*, p. 556) the question whether the increased transpiration which generally follows the relief from compression is really due to the opening of the stomata, or whether the sudden rush of water into the leaf could produce the effect, even though the stomata remained half closed. I see no way of deciding the question.

LIGHT AND DARKNESS.

I made a considerable number of experiments on the diurnal opening and closing of the stomata, using as a control either a leaf whose stomata remain open at night, or an artificial leaf made of damp linen, or a withered leaf. The curves obtained show clearly enough a lowering of the temperature at sunrise, and a rise at sunset, but I have gradually come to think the results not sufficiently trustworthy to be published, and for the present I withhold them.

ARTIFICIAL CHANGES IN ILLUMINATION.

The most interesting results were obtained by artificial darkness. In my early experiments the plan followed was to fix a large horizontal sheet of glass close above the bulbs of the recorder which were placed as near as possible to each other. By covering the glass with black cloth, a considerable diminution in illumination could be produced without any danger of altering the hygroscopic conditions of the air.

Afterwards I managed to produce a greater degree of darkness by adding a curtain, hanging down like a flounce, all round the glass plate. As long as the horizontal glass was uncovered the leaf on the recorder bulb was well-illuminated, as the experiments were made in a greenhouse. When the black cloth was drawn over the horizontal glass the light was sufficiently diminished to produce rapid closure of the stomata; at the same time the other physical conditions are not altered in such a way as to produce a difference in temperature between the two bulbs. In order to make sure that the increase in the leaf temperature (which occurs in darkness) is actually due to stomatal closure and not to purely physical effects, several experiments were made with "artificial leaves." The two bulbs, wet and dry, were placed close together under the flounced glass plate, one bulb being covered with damp linen, the other being left naked, or covered with dry paper on platinum. The effect of alternating periods of light and darkness on the relative temperature was uncertain and variable, and in this respect very different from the results obtained with living leaves. The results with artificial leaves were as follows:

Exp. 79.—There was either no effect on the temperature, or when an effect was produced it was the reverse of the leaf-effect, *i. e.*, the artificial leaf became relatively cooler in darkness, warmer in light.

Exp. 86.—No definite effect on the temperature-curve.

Exp. 89.—The effect of alternate light and darkness was perceptible, and was of the same character as in the case of leaves, *i. e.*, darkness produced a relative rise of the temperature of the artificial leaf. But the curve as a whole is strikingly different from a leaf-curve, both in the slight amplitude and the slow occurrence of temperature change.

Exp. 96.—Four alternate observations of light and darkness produced no visible effect on the relative temperature.

From these experiments I conclude that alternations of light and darkness do not produce alternations in the temperature of a layer of wet linen. This being so, we may, I think, accept the obvious explanation that the temperature changes produced in a living leaf are simply due to opening and closing of the stomata.

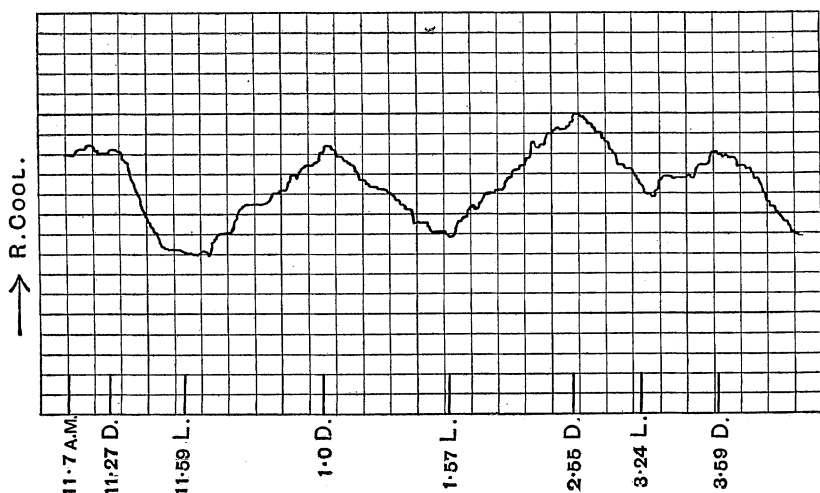


FIG. 14.

EXPERIMENT 62, fig. 14. March 27, 1900. NARCISSUS.

The leaf on bulb R, an artificial leaf on B; therefore, an R-cool rise in the curve means an opening of the stomata.

The diagram shows the times at which the illumination was

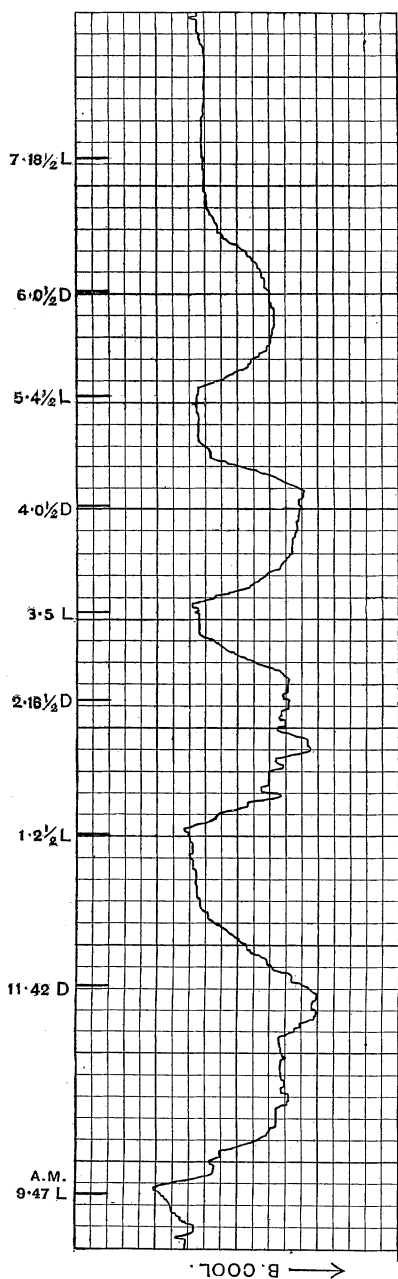


FIG. 15.

changed, D meaning that the black velvet was drawn over the glass, L that it was removed.

The first two changes at 11:27 and 11:59 A. M. take place somewhat slowly, *i. e.*, from 6 to 10 minutes after the change in illumination, but the later variations in the curve coincide very closely with the letters D and B. The R-cool change at 3:24 is smaller than the others. This is probably an instance of what is usually quite obvious, that late in the afternoon the stomata do not open when illuminated.

EXPERIMENT 77, *fig. 15.* May 23, 1900.

CAMPANULA PYRAMIDALIS.

Campanula on bulb B, withered leaf on R; a B-cool fall in the curve means opening stomata.

As in *fig. 14*, the letters D and L give the times at which the black velvet was replaced or withdrawn. The reaction time varies somewhat through the day, but in many cases the change in the curve follows very closely the change in illumination. At 7:19, *i. e.*, 40 minutes before sunset, the removal of the black cloth produced no effect. In my *Observations on stomata*, p. 596, I called attention to this fact, so that in this respect *fig. 15* and other similar results confirm my former work. But this refusal of the stomata to open at a time approximating to their natural hour for closing is the

only evidence of periodicity which I have obtained. It corresponds exactly to some of Pfeffer's experiments on the "sleep" of flowers.¹³ On the other hand, my curves do not confirm the more detailed differences between the behavior of the stomata in the morning and afternoon, as given in my *Observations* at the foot of p. 596. This is a difficulty which I hope to clear up.

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¹³ *Physiol. Untersuchungen*. 1873.